Title: The biology of color

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Abstract:

Coloration mediates the relationship between an organism and its environment in important ways, including social signaling, anti-predator defenses, parasitic exploitation, thermoregulation, and pigments offer protection from ultraviolet light, microbes, and abrasion. Methodological breakthroughs are accelerating knowledge of the processes underlying both the production of animal coloration and its perception; experiments are advancing understanding of mechanism and function; while measurements of color collected noninvasively and at a global scale are opening windows to evolutionary dynamics more generally. Here we provide a roadmap to these advances and identify hitherto unrecognized challenges for this multi-disciplinary field.

One sentence summary: Current status and future prospects for multidisciplinary research in the field of animal coloration.

Introduction

The study of animal coloration has a venerable history. During the 19th century early evolutionary biologists set out to explain the diversity of colors they observed as products of natural selection (*1*). The 20th century saw color phenotypes adopted as genetic markers contributing to our understanding of development, genetics and evolutionary theory. In the last two decades the field has again witnessed explosive growth. Coloration provides exceptional access to phenotypic diversity because we can quantify how color is perceived by visual systems of diverse species, and humans are visual animals. Contemporary technologies enable biologists to investigate both nanoscale and cellular mechanisms producing color, the sensory, neural, and cognitive bases of color perception, and the adaptive significance of external appearances. Progress in each area is rapid, making animal coloration an exciting interdisciplinary field but difficult to keep pace with.

Mechanisms of color production

Colors in animals and plants are produced by pigments and nanostructures (*2*). While knowledge of how mechanisms manipulate ultraviolet (UV) to infrared wavelengths is accumulating (*3*), we currently lack an appreciation of the developmental processes involved in cellular structure and pattern formation at optical scales (nanometers to microns). Nonetheless, the field of soft condensed matter physics (*4*) holds great potential for new insights into optical architectures. This will be a critical foundation for future understanding of ordered self-assembly in colored biological materials from beta-keratin in birds' feathers (*5*) to chiral or uniaxial chitin structures in beetles (*6*). Such knowledge can illuminate the costs, constraints and evolution of coloration.

Across animals, coloration serves as a dynamic form of information (**Fig. 1**). Colorful body parts are moved via behavior and both pigments and structural colors change at various temporal resolutions (*7*). Cephalopods are perhaps the most famous example (*8*), but mobilization of pigments and nanostructures to change coloration is taxonomically widespread. Considerable opportunities exist for dissecting color pigment movements (*9*) and in manipulating their hormonal or neural control (*10*). Dynamically changing structural coloration can also manipulate the polarization of light (*11*). There will be exciting discoveries regarding how animals perceive polarization and integrate it with color information (*12*, *13*).

While structural colors occupy a huge area of color space, pigments are limited by chemistry (*14*). Furthermore animals lack many pigment synthesis genes common to plants. Most famously, animals cannot manufacture carotenoids, but the genes and enzymatic pathways involved in the modification of carotenoids into those that are used to create a range of colors are only now under scrutiny (e.g. *15*). Lateral gene transfers may be involved: aphids, for example, incorporate fungal genes to produce a wider spectrum of carotenoids (*16*).

Genetics of color and evolutionary change

In studies of variation in animal coloration, there was an early emphasis on understanding the consequences of coding sequence changes, such as at the MC1R gene that regulates melanin production (*17*), but advances in color genetics focus on regulatory changes which can underlie co-option of genes into novel functions. For instance, a ketolase enzyme that evolved to modify carotenoid pigments in the retina of birds paved the way for the expression of red pigments in bills and plumage (*17*); similarly the *Alx3* transcription factor has come to regulate the expression of melanocyte differentiation in striped rodents (*18*).

Genes underlying color variation offer insight into the predictability of evolution. Convergent phenotypes commonly arise in parallel; the accurate characterization of color phenotypes has revealed independent changes in similar genetic mechanisms leading to phenotypic similarity between species (*19*). For example, changes in pigmentation from weakly to deeply melanic can be controlled by parallel genetic changes in highly divergent lineages, such as the Kit Ligand in pigmentation of sticklebacks and human skin color, Oca2 in pigmentation of snakes, cavefish and humans, and MC1R in numerous birds and mammals (*19*). There has been evolutionary bias towards repeated use of the same genes perhaps because these represent mutations with the smallest pleiotropic effects (*19*).

Convergence is also relevant to the genetic and developmental processes that bias, constrain, or facilitate evolutionary diversification. Artificial selection in *Bicyclus* butterflies show how some wing-pattern traits are constrained, while other patterns can be selected in directions unexplored in natural populations (*20*). In *Heliconius* butterflies, shuffling of enhancer elements through introgression and recombination can produce phenotypic diversity on a short timescale, without novel mutations (*21*).

Discrete color phenotypes are often associated with differences in morphological, physiological and behavioral traits. If selection favors specific trait combinations, it can generate genetic correlations representing alternative adaptive peaks (*22, 23*). In some cases, this can lead to the evolution of single locus control of co-adapted traits, “supergenes” (*24*), and there are striking examples of mimicry (*25*) and sexually selected coloration (*26*) involving elements linked by chromosomal inversions. So the genetic mechanisms of color variation can therefore offer insights to the adaptive evolution of genome structure.

Genomic insights will prove valuable in investigations of mechanisms by which colorful traits honestly signal individual quality (*27, 28*). It is widely accepted that a

sexual ornament can reveal quality, because of the challenges associated with producing or bearing such traits (*29, 30*), but we remain largely ignorant of the mechanisms that underlie gene-by-environment interactions causing condition-dependent signaling. Epigenetic studies at the genome scale may offer insight into this question.

Knowledge of genetic mechanisms underlying the creation and transport of pigments, such as melanin and carotenoids, has advanced considerably in the last 15 years (*23*) but outstanding questions for structural coloration remain. Understanding the genetic control of size and shape dispersion is important because these properties ultimately control optical structures. An appreciation of the genetics of nano-structural color production could also be important for biotechnological applications, for example creation of sensors and reporting mechanisms.

Receptor processing and cognition

The way in which humans think about color is influenced by our own abilities and experience, but it is now widely appreciated that animals have different visual abilities: e.g. insects and birds see UV and birds have more than three retinal cones types; some fish even change color vision with diet (*31*) and utilize chlorophyll in far-red sensing (*32*). We conceive of color as a percept with attributes of hue, saturation and lightness but other species may process receptor information differently. Indeed, even the common practice of modeling color as a geometric space or volume with a dimension matching the number of interacting photoreceptors types (*33*) may be an unwise assumption. For example, butterflies have what appears to be 'conventional' tri- or tetrachromatic color vision, yet have spatially distinct receptors that seem dedicated to specific tasks. In the swallowtail butterfly *Papilio xuthus* there are at least six spectrally distinct photoreceptor types. Green-sensitive receptors in the

distal retinal layer process high frequency information achromatically for motion vision; the same photoreceptor class in the proximal layer of the eye contributes to color vision (*34*). More generally, many invertebrates and vertebrates have different vision sub-systems, each tuned to one specific task. Local receptor concentrations analyze particular spectral wavebands in precise regions of the visual field; for instance, UV and/or polarization patterns in the skyward-looking part (*35*). Perhaps the most striking case where the rules of 'normal' color vision do not apply are stomatopods (mantis shrimps); these have many photoreceptor classes (up to 12) but relatively poor color discrimination ability (*36*) **(Fig. 2)**.

Neuroethologists have long studied circuits underlying visuomotor and phototactic responses but comparable systems are almost unknown in color vision. Color opponent neurons that compare photoreceptor responses are thought essential to color vision, and have been recorded from many animals but, even in primates, later stages of neural processing are poorly understood (*37*). Apparently fundamental processes such as color constancy (the relative invariance of object color despite changes in the spectrum of the illuminant), documented in many animals (*33*), is achieved via multiple mechanisms. In humans, percepts of color are also influenced by perceived surface texture, local configuration, context and prior associations (*38*); such effects in other species are poorly researched. How color is integrated with other sensory information and motor systems is also opaque. One of the few examples is the locust's *Schistocerca gregaria* celestial compass, where the neurons of the central complex integrate polarization intensity and charismatic cues to locate the sun (*39*). More research on the neural mechanisms by which color influences behavior is our next challenge.

Integrating color, pattern and motion

Visual ecologists have traditionally focused on uniformly colored static signals. However, many animal signals are complex and dynamic in both space and time, with spatial patterning (markings) and strong motion-based components (**Fig. 1**). As illustrations, motion is central to the signal of iridescent wings of the damselfly *Megaloprepus caerulatus* (*40*) or tail of jacky dragon lizards *Amphibolurus muricatus* (*41*). Relatively little is known about how different animals perceive and recognize patterns in motion, let alone integrate motion, contrast and color in signaling; lack of quantitative methods has been a major limitation. Pattern recognition algorithms revolutionizing analyses of pattern (e.g. *42, 43*) and motion (*44*) should be the next target of investigation. Understanding how animals vary in their temporal visual resolution – and how this influences the perception of moving displays – is now a tractable question using off-the-shelf high-speed cameras. Moving forward, it will also be critical to determine which methods of pattern and motion analysis best resemble biological vision.

Despite the ubiquity of color-based communication in diverse behavioral model systems, mechanisms of higher level neural processing and decision-making remain unexplored in natural contexts. This stands in contrast to vocal communication, where many neuro-ethological techniques, including physiological recordings and fMRI in behaving and alert subjects, have been applied to songbirds (*45*). Some of these techniques should be transferable to visual communication and even taken into the field. We recommend intensifying investigation of visual and cognitive processing of animal coloration using neuro-ethological techniques, from eye-trackers and non-invasive neural imaging to temporary inactivation of putative constituents of visual neural circuits (e.g. *46*).

Mechanisms of vision and visually guided behavior should be studied top-down as well as bottom-up. A benefit of the former is being able to predict and observe differential behavioral responses to similar color signals in different ecological contexts. For example, great reed warblers *Acrocephalus arundinaceus,* frequent hosts of the common cuckoo *Cuculus canorus*, show context-dependent rejection of foreign eggs (*47*) (**Fig. 3**). Mimetic eggs are typically accepted by these hosts, but in the presence of a cuckoo near the nest, or after exposure to a non-mimetic cuckoo egg, these same eggs are often rejected. Understanding how the host cognitive system adjusts its recognition thresholds to accommodate increased risks of cuckoo parasitism needs attention (*48, 49*).

Color interactions with other sensory modalities

By determining how color patterns excite visual receptors in appropriate light environments, models of color vision allow us to predict how color signals appear to receivers (*50, 51*). If we want to understand the evolution of animal coloration, however, studying color patterns in isolation can mislead. The visual complexity of the background affects the detection of cryptic prey independently of the prey's camouflage per se (*52, 53*). Importantly, visual properties can be substantially affected by other sensory modalities. For instance, swallowtail butterfly responses to colors are modified by host plant odors (*54*). Effects can be simple, such as drawing attention to a visual signal/stimulus, but alternatively they can depend on the difficulty of the visual task (e.g. *55*). Electrophysiology and neuro-imaging studies are beginning to explain cross-modal effects on visual attention (*55, 56*). To date, such studies have been conducted on a limited number of species (flies, rats and humans) with findings slow to filter through to models of visual perception.

Non-visual sensory information alters how receivers respond to color signals. Aposematic prey that advertise their toxicity to predators using conspicuous coloration often additionally use odors, sounds and tastes. These non-visual modalities enhance innate biases against colors typically associated with aposematism (red, yellow, black), potentiate the learned association between prey color and toxicity, and enhance retention of these learned associations (*57*). Determining how non-visual components of both signals and signaling environments affect receiver perception, cognition and behavior will identify the full gamut of selection pressures acting on animal color patterns (*58*) and, indeed, the influence of environmental change (*59*)**.** Although there are examples of how color signals and receiver visual receptors have coevolved in particular light environments (*51, 60, 61*), we need to understand coevolutionary relationships when signals are multi-modal or produced in the presence of non-visual environmental noise.

Multiple functions of color

Researchers usually try to identify single key functions of external appearances (*1*), but individual color patterns can experience multiple, often opposing, selection pressures (**Fig. 4**). Several solutions have evolved to allow organisms to cope with these. The latitudinal gradient of human skin pigmentation, for instance, reflects two clines: one emphasizes protection against high UV radiation through permanent eumelanin-based pigmentation; the other promotes absorption of UVB (280–315 nm waveband) for vitamin D photosynthesis in low or highly seasonal UV environments through depigmented skin (*62*). Variation in skin color and tanning ability between populations represents a compromise between these conflicting pressures (*63*). A related trade-off has been demonstrated in avian eggshells where blue-green biliverdin pigments block harmful UV from entering the egg but minimize overheating through thermal absorption (*64*).

Likewise, although one might expect that color patterns that help conceal potential prey and warn predators on their discovery would be incompatible, these functions are not necessarily compromised; perceived color is distance-dependent (*65*). For example, highly contrasting colors can blur into the background when viewed from afar, but become conspicuous and contrasting when observed at shorter distances (*66*). Whether and how organisms resolve trade-offs will depend on the shape of the fitness curve resulting from different selective forces.

Changing color is an obvious strategy when individuals encounter different habitats, grow in size rapidly or encounter new predators over time (*7*). Some color displays are behaviorally triggered and only shown when a predator is very near (e.g. katydids with deimatic displays (*67*)). Some cuttlefish change color and shape according to the predator species (*68*), while crabs change color over hours to match a new background (*69*), as do many other invertebrates over longer timescales. For example, alder moths *Acronicta alni* show ontogenetic change from masquerade (of bird droppings) to aposematism when they need to move and pupate (*70*). Finally, mammals, like deer, are born with striped coats but take on uniform pelage as adults (*71*). These temporal solutions are expected to arise in response to predictable spatial or temporal changes in selection pressures (*72*).

Another solution to different selection pressures is polymorphism. This is most evident in sexual dimorphism but it also occurs within the same sex as a consequence of multiple selection pressures; e.g. to escape harassment (*73*), to obtain a mate (*74*), or to remain cryptic to multiple predators (*75*). Selection for alternative phenotypes within the same population may arise by frequency dependent selection (rare morph advantage), heterogeneous selection in space or time, or heterozygote advantage (*76*).

The same color pattern can be perceived differently by different receivers, and this can be exploited by organisms to resolve different challenges simultaneously (*77*). This includes private channels of communication, whereby a signal is more salient to intended receivers (e.g. potential mates) than to unwanted observers (e.g. predators). For example, some damselfish possess UV face patterns that facilitate individual recognition for territoriality, while remaining largely hidden to UV-insensitive predators (*78*). Hidden channels can also involve other visual modalities; some mantis shrimps use circularly polarized patterns, invisible to other species (*79*). Thus far, however, few experiments have used behavioral tests of eavesdropper detection to assess predictions from vision modeling.

Like private communication, organisms can also separate signals spatially (**Fig. 4**), such that different parts of the body convey different information. For example, many animals have dorsal coloration that reduces predation via crypsis or aposematism, but ventral coloration for short range intraspecific signaling (e.g. *80*). These mechanisms are likely to be common when multiple receivers perceive the signaler from different directions.

Color in space and time

Attempts to understand variation in animal coloration patterns across time and space go back to Wallace's (*81*) investigation of color brilliance of birds and butterflies in tropical and temperate zones. Until recently, most comparative analyses of coloration were small-scale, largely because of restricted datasets or computational power limitations. Recently there has been a concurrent onset of "big data" approaches in remote sensing (*82*), well-resolved phylogenies (e.g. *83*), and novel methods for quantifying large numbers of diverse color patterns (*42, 43*), combined with new analytical methods to integrate these datasets (*84*). Coupled with new research

areas such as paleo-coloration (*85*), a broad picture of color pattern evolution across space and time can be generated. For example, spectral, ecological and thermal data at large spatial-temporal scales can be used to explain epidermal pigmentation in people (*63*).

The ways in which biotic and abiotic factors interact to affect color pattern diversification across species can be investigated using knowledge of species' spatio-temporal distributions and phylogenetic relationships. For example, avian coloration is more divergent at intermediate levels of sympatry, where competition between species may select for distinctive patterns, whereas at higher levels of range overlap, relaxed selection or ecologically driven convergence reverses this pattern (*86*).

Recently, Davis Rabosky et al. (*87*) combined geographic, phylogenetic, ecological, and coloration data in an integrated spatio-temporal analysis of a classic mimicry complex: New World coral snakes and their Batesian mimics (**Fig. 5**). While model and mimic color patterns were correlated in both space and time as predicted, demonstration that mimicry is gained and lost frequently challenges the idea of it being a stable 'end-point'. Moreover, this high-quality dated phylogeny conclusively demonstrated that coral snake mimics do indeed arise subsequent to the evolution of coral snakes, and geographic data pinpointed where this occurred.

That pigmentary and structural coloration are regularly preserved in fossils was only established recently, and fossil markers provide a dated reference for the advent of different aspects of coloration (*85*). Already investigations have identified color and pattern phenotypes, production mechanisms, and even color function (*85, 88*). Mechanisms of color production are highly conserved, and functions such as anti-

predator camouflage were likely in use in the Cambrian, indicating the earliest existence of visually oriented predation (*85*).

Conclusion

Since color is an easily measurable and labile character, studies have used it for understanding evolutionary processes since Bates and Wallace (*89, 90*) but only recently have visual physiologists, sensory ecologists, behavioral ecologists, and evolutionary biologists with shared interests in coloration come together to study the mechanisms of production and perception, the intricacies of function, and patterns of evolution (*91*). Moreover, color patterns and color polymorphism are both associated with speciation dynamics (*92*). We are on the threshold of a new era of color science and the interdisciplinary nature of this collaborative enterprise holds enormous promise.

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Figure legends

Fig. 1. Iridescence allows vivid, dynamic, view-dependent signals.
The iridescent throat of this Broad-tailed Hummingbird (*Selasphorus platycercus*), the feathers of which are structurally colored, changes dramatically in appearance from black to magenta based on the viewing angle and/or the angle of illumination. The bird on the left is the same as the bird on the right. © M. C. Stoddard.

Fig. 2. Multi-spectral vision in the mantis shrimp.

A stomatopod crustacean, *Gonodactyulus smithii*, showing off species-specific meral spots. These reef-dwelling mantis shrimps possess photoreceptors covering 12 spectral wavebands and have coloration as elaborate as their vision might predict. This display may be both a warning display and a mate attraction display. © Roy Caldwell.

Fig. 3. Visual discrimination and egg rejection by cuckoo hosts.
Common cuckoos (*Cuculus canorus*) parasitize Great Reed Warblers (*Acrocephelus arundinaceus*) with closely mimetic eggs, but a third of these eggs (bottom two) are still rejected. Visual context-dependence influences the cuckoo egg's chance of removal: the sighting of an adult parasite by the host near the nest increases, whereas multiple parasitism by two or more foreign eggs reduces rejection rates *(45)*. © Csaba Moskat.

Fig. 4. Multiple ways in which coloration promotes survival and reproductive success.

From left to right and top to bottom: African mocker swallowtail *Papilio dardanus* © Simon Martin, showing female-limited Batesian mimicry to different unpalatable models (top two butterflies) but males are undefended non-mimics (bottom). Spotted lanternfly *Lycorma delicatula* © Changku Kang, is a cryptic toxic planthopper at rest, with wings folded vertically, but aposematic in flight displaying its conspicuous red hindwings. Dyeing dart frog *Dendrobates tinctorius* © Jim Barnett and Constantinos Michalis, is highly poisonous and conspicuous but also sexually dichromatic indicating sexually selected coloration for mate choice. Wood tiger moth larvae, *Parasemia plantaginis* © Johanna Mappes, are aposematic with darker individuals found in more northern latitudes to warm up quickly but they suffer greater predation. Paper wasps, *Polistes dominulus* © Elizabeth Tibbetts, signal dominance by extent of black on the yellow portion of their heads, and sport characteristic yellow and black aposematic integument. Male impala, *Aepyceros melampus* © Tim Caro, is a countershaded antelope that also matches its background. Cuttlefish, *Sepia officinalis* © Keri Langridge, can rapidly change color to match their background as well as signaling aggression and interest in the opposite sex. Barn owls, *Tyto alba* © Alexandre Roulin, have dark and pale reddish pheomelanic morphs that are differentially successful in catching rodents according to habitat presumably because of differential crypsis; darker feathers are more resistant to wear which may allow different flight behavior. Giant pandas, *Ailuropoda melanoleuca* © Theodore Stankowich, have faces to signal to conspecifics but black and white body pelage for crypsis in snow and shade. Male lions, *Panthera leo* © Craig Packer, with darker manes are preferred by lionesses and approached more cautiously by males compared to blond conspecifics. House finches, *Haemorhous mexicanus* males © Geoffrey Hill, sport red plumage preferred by females and that reflects extent of coccidial and mycoplasmal infections. Guenons, here *Cercopithecus mona* and *C. sclateri* © Will Allen, show greater facial complexity in larger social groups perhaps for individual recognition and have distinctive faces from sympatric heterospecifics to facilitate species recognition. Human, *Homo sapiens* © Nina Jablonski, skin color is a compromise between avoiding damage from UVB radiation at low latitudes and manufacturing vitamin D in highly seasonal UV environments. House sparrow, *Passer domesticus* © Geoffrey Hill, bib size and blackness signal dominance in flocks of wintering birds and reflect higher levels of immunocompetence during the non-breeding season. Willets, *Catoptrophorus semipalmatus* © Bruce Lyon, have white livery perhaps to coordinate flight movements when they take off together in

large groups, confuse predators or increase aerodynamic efficiency. Montage by Laszlo Talas.

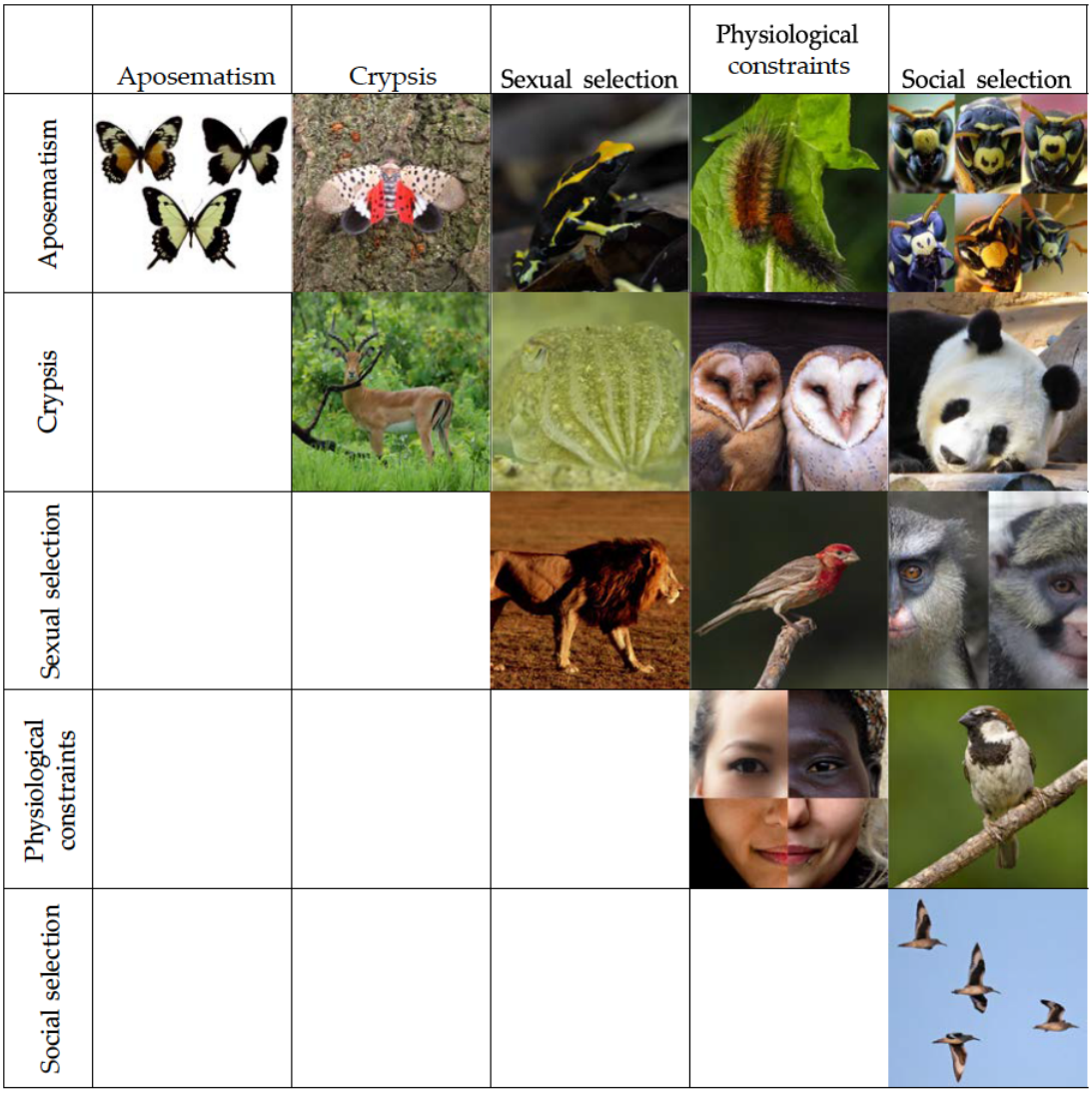

Fig. 5. An aposematic coral snake and its harmless mimic.

Highly venomous coral snakes (such as *Micrurus annelatus*, left © Roy Santa Cruz Farfán) display bright aposematic coloration that is mimicked by harmless snakes (such as *Oxyrhopus petola*, right © Pascal Title) across the Western Hemisphere (*87*).